# IMPERFECTION OF POLLEN AND MUTABILITY IN THE GENUS ROSA*

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(WITH PLATES IV–VI)

During the winter of 1915–1916 I made a study of all the species, of which specimens were obtainable, of the genus *Rosa*. This was done in connection with work on other genera of the family Rosaceae, notably on *Rubus* and on *Crataegus;* and it has been interesting to note that in all 3 genera there is indication of a large amount of hybridism, and that the multiplication of species is startlingly great.

From the Arnold Arboretum of Harvard University, I have been able to obtain flower buds of 32 different species of *Rosa*. Of 3 of these species I have several varieties; 5 varieties of *R. spinosissima*, 3 of *R. rugosa*, and 2 of *R. virginiana*. The buds were taken when on the point of opening, thus making sure of the maturity of the pollen. They were then preserved in alcohol until such time as it was possible to examine them.

I prepared sections of about half of the species gathered, with a view to determining how many showed sound pollen and how many showed a greater or smaller proportion of undeveloped or imperfect pollen. For this purpose the buds were first imbedded in celloidin to make sure that there would be no shrinkage of the parts. Sections were cut with the microtome, stained with Heidenhain's haematoxylin and safranin, and finally mounted in balsam.

For nearly a century it has been known that one of the most important and most easily recognized characteristics of a hybrid is imperfect pollen. DUTROCHET[1] in 1832 recognized the morphological sterility of the hybrid and pointed out that pollen abortion is a criterion for hybridism. GAERTNER,[2] in 1849, speaks of the

*Contribution from the Laboratories of Plant Morphology of Harvard University.

[1] DUTROCHET, HENRI, Sterility of hybrid plants. Gard. Mag. 8:500. 1832.

[2] GAERTNER, C. F., Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich. Stuttgart. 1849.

importance of the pollen conditions in determining the fertility of a hybrid as follows:

Die wichtigste Theil der Befruchtungstheile der Bastarde ist der Pollen. Es ist nun aber zu bemerken, dass ein vollkommen normal gebildeter Pollen sein Ovarium nicht absolut zu befruchten vermag, weil manche mit wirklich potentem Pollen bestäubte Blumen nicht selten doch abortiren und unbefruchtet abfallen: obgleich in der Regel von dem Vorhandensein eines vollkommenen Pollens bei den reinen Arten auf die Fruchtbarkeit einer Pflanze geschlossen werden darf.

Since, therefore, imperfect pollen is a well known characteristic of hybrids, and one of the easiest means of identifying them, it is from an examination of the pollen of the species of *Rosa* that their probable genetical status can be determined most easily. The thin sections through the anthers, when examined microscopically, give one a remarkably clear view of the pollen grains in all positions in anthers in all parts of the different buds.

GAERTNER is again in harmony with our modern ideas in his observations concerning the difference between perfect and imperfect pollen grains, or, as he calls them, fertile and infertile; for even a hybrid may have the means, however imperfectly developed, of reproducing its kind. GAERTNER states as follows:

Die Gestalt und Grösse der Körner des Pollens der Bastarde in der nämlichen Anthere ist weit mehr verschieden, als man es nach FRITZSCHE und H. V. MOHL in den der reinen Arten zuweilen antrifft.

In den Antheren aller fruchtbaren Bastarde, befinden sich kleinere und grössere Körner mit einander vermischt in verschiedenen Verhältnissen zum Theil äusserst kleine von verschiedenen Graden der Unförmigkeit länglichte, eingeschrumpfte, leere Bälge, ohne flüssigen Inhalt—am deutlichsten findet man dies bei solchen Individuen, welche eine geringe Fruchtbarkeit besitzen. . . . . Aus der Grösse und Qualität der Pollenkörner kann man daher in manchen Fällen mit ziemlicher Zuverlässigkeit auf die Fruchtbarkeit oder Unfruchtbarkeit eines Bastards schliessen.

Die reine Farbe bezeichnet in den meisten Fällen die Potenz des Pollens.

Die Verstäubung des Pollens der Hybriden ist wie schon bemerkt sehr mangelhaft; er vertrocknet häufig in den Antheren, wenn sich diese auch öffnen.

Der Inhalt des Pollens der Bastarde ist sehr verschieden und auch selbst bei den fruchtbaren gering, meistens fehlt er aber gänzlich und der Pollen ist dann trocken und ballt sich nicht. . . . . Wenn der Pollen seine regelmässige Gestalt und Grösse hat so enthält er gewöhnlich eine flüssige ölige Materie.

That is, normal pollen is perfect morphologically, fully formed, and having normal protoplasmic contents; while abnormal or imperfect pollen, such as often characterizes known hybrids, on the contrary, is usually shrivelled and has little or no protoplasmic contents, consequently making the grain quite impotent.

The pollen of *Rosa* is largely in the last named condition, imperfect, and therefore probably sterile to a considerable extent. Of the 32 species secured from the Arnold Arboretum, 2 show entirely perfect pollen, and in 3 others imperfectly developed grains were slightly intermingled; that is, showing only 1–10 per cent bad pollen. Seventeen show a very large percentage of imperfect grains (about 50–100); and the remaining 20 show 10–50 per cent.

This enormous degree of infertility of pollen in the genus probably accounts for much of the difficulty systematists seem to have encountered in establishing species. ENGLER and PRANTL[3] speak of the genus thus:

> Die allbekannte, von Dichtern aller Kulturvölker gepriesene Rose bildet eine scharf umgrenzte Gattung, die sich durch den Bau der Blütenachse den Sanginsorbeae und Pomoideae, durch den übrigen Blütenbau den Potentilleae durch die Tracht insbesondere der Gattung Rubus anschliesst. Sie ist fast über die ganze nördliche gemässigte Zone verbreitet, geht auch in die Gebirge der Tropen über, fehlt jedoch auf der Suedl. Halbkugel.
>
> Die Zahl der Arten kann man bei mittelweiter Fassung des Artbegriffes auf etwa 100 ausschlagen, doch sind schon allein aus Europa mehrere hundert Arten niederen Ranges beschrieben worden.

The last edition of GRAY'S *Manual* recognizes 15 species of wild roses of the eastern United States and Canada, and in the last edition of *Field, forest, and garden botany*, in which are included cultivated species and varieties, there are 24 species.[4] Nine of the wild species, so-called, of GRAY (M.), I have been able to obtain from the Arnold Arboretum, also 4 of the cultivated species. The 20 odd species remaining that I have analyzed are importations, hybrids, etc., grown specially in the Arboretum. Of the 3 divisions made of the species of *Rosa* according to the percentage of bad pollen present, I shall first take up the group in which the proportion was

[3] Die natürlichen Pflanzenfamilien (p. 46).

[4] In the following pages the *Manual* is indicated by (M.), and *Field, forest, and garden botany* by (F.F.G.).

less than 10. In this group are *R. rugosa*, *R. cinnamomea*, *R. Kelleri*, *R. pendulina*, and *R. Moyesii*.

*R. rugosa* (figs. 5, 13) has almost no imperfect grains as may be seen in the figures, practically all of the grains being perfectly formed and full of protoplasmic contents. Fig. 5 shows the pollen teazed out of the anthers on to a slide. Fig. 13 is a cross-section through an anther, showing the pollen grains in their normal positions in the loculus of the anther. It is worth while to note also the generous quantity of pollen in the single loculus. GRAY (F.F.G.) groups *R. rugosa* among the principal types of exotic garden roses which are "much mixed by crossing and changed by variation." The reason, doubtless, for the purity of *R. rugosa* as compared, for instance, with *R. rubiginosa* (fig. 6) is its geographical seclusion on the islands of Japan. The varieties of *R. rugosa* show evidence of contamination, as will be shown later.

*R. cinnamomea* and the 3 other species in this group (*R. Kelleri*, *R. pendulina*, and *R. Moyesii*) have not been figured. All may be found in the Arnold Arboretum. They are all practically without imperfect pollen grains. *R. pendulina* comes from the mountains of Europe, and *R. Moyesii* comes from China.

In the second and much larger group the percentage of imperfect pollen is 10–50. In this group are *R. spinosissima altaica*, *R. spinosissima* (garden variety hybrid), *R. spinosissima*, and *R. spinosissima hispida;* also *R. spinosissima paniculata* (garden variety). *R. spinosissima fulgens* (garden variety), because of its larger percentage of undeveloped grains, belongs to the third and last group. With these are *R. Harrisoni* (garden hybrid), *R. gymnocarpa*, *R. Manetti* (garden hybrid), *R. blanda*, *R. seraphini*, *R. wichuriana*, *R.* no. 306 Wilson, *R. pratincola*, *R. multiflora*, *R. davurica*, *R. acicularis*, *R. hemispherica*, and *R. ferruginea*. Of *R. rugosa alba* and *R. virginiana alba*, which properly belong in this group, I shall speak later in connection with other varieties of the same species in the third group.

*R. spinosissima* and its 5 varieties present some very interesting conditions. Fig. 12 is a cross-section of the typical anther of the so-called species. It is very clearly seen that about 40 per cent of the grains in the loculus are shrivelled and without protoplasmic

contents; and the contrast between these and the perfect grains is very marked.

In comparing the species *R. spinosissima* with the recognized garden hybrid, a variety of the species and called *R. spinosissima* garden variety hybrid (fig. 10), the latter shows less pollen in the loculus, but about the same percentage of shrivelled grains. *R. spinosissima paniculata*, another garden variety, has only about 10 per cent of its pollen grains undeveloped; while still a third garden variety, *R. spinosissima fulgens*, has a larger percentage than any of the group I have examined. This last, as may be seen in fig. 11, has an abundance of pollen grains in the loculus, but about 50 per cent of them appear as tiny, shrivelled cells.

The two remaining varieties of *R. spinosissima*, *R. spinosissima altaica* and *R. spinosissima hispida*, are apparently the least contaminated of the varieties. The first, a Siberian rose (fig. 8), has a considerable amount of pollen in the loculus, and only about 10 per cent of its grains are bad. The second (fig. 9) presents an almost identical situation; and this is a European variety of the same species.

The next species in the group is *R. Harrisoni*, a recognized garden hybrid. Fig. 18 shows the poorly developed pollen typical of this species, about 40 per cent of the grains being imperfect if not entirely shrivelled. GRAY (F.F.G.) described "*R. Eglanteria* L. a yellow Eglantine rose. Like a sweetbriar, but lower. Austrian briar, Persian yellow, and Harrison's yellow are forms of this." I have not been able to obtain specimens of *R. Eglanteria* L., the parent, but certainly the offspring is an excellent example of the condition of badly developed pollen usually accepted as indicating hybridism.

*R. Manetti*, another garden hybrid (fig. 17), presents a condition analogous to that found in *R. Harrisoni*. *R. gymnocarpa*, a northwestern North American rose, is much less contaminated than the last two, only about 20 per cent of its pollen grains being imperfect.

The remaining species of the group under discussion present conditions more or less similar to those already described. *R. blanda* has about 20 per cent bad pollen; *R. seraphini* has only about 10 per cent; *R. wichuriana* has numerous shrivelled grains;

*R.* no. 306 Wilson, a Chinese wild rose, shows about 15 per cent bad pollen; *R. pratincola* has about 25 per cent of its pollen grains undeveloped; *R. multiflora* has about 20 per cent bad pollen. The last is a rose native to Japan and China, and cultivated here. GRAY (F.F.G.) records it among the principal types of exotic garden roses: "*R. multiflora* Thunb. from Japan and China. Hardy in the Middle States, a double form of an old garden rose, the single form not common. Polyantha roses are offshoots of this chiefly through hybridization with *R. indica*."

*R. davurica* is a Siberian rose which shows more imperfection of pollen than *R. spinosissima altaica*, having 25–30 per cent of its pollen undeveloped, in contrast with 10 per cent in the other species. *R. acicularis*, another rose native to Siberia, is in a similar condition of probable contamination; this species is now wild in the Northern Hemisphere. *R. hemispherica* is a Persian yellow rose, probably like *R. Harrisoni*, an offspring of *R. Eglanteria*. I examined the variety *R. hemispherica plena*, and found the pollen in bad condition. The last of the species in the group is *R. ferruginea*, native to the mountains of central Europe, and here also the pollen was to a large extent abortive, a condition interesting when compared with that found in *R. pendulina*, likewise a native of the European mountains, but almost without bad pollen.

In the third group are those species with 50–100 per cent bad pollen. This group is not quite as large as the second group, but presents conditions even more interesting. It includes *R. kamchatica*, *R. cordifolia*, *R. rugosa plena*, *R. rugosa alba*, *R. rugosa arnoldiana*, *R. oxyodon*, *R. rubiginosa*, *R. setipoda*, *R. mollis*, *R. macrophylla*, *R. canina biserrata*, *R. arvensis*, *R. gallica*, *R. alba*, *R. damascena*, *R. virginiana plena*, and *R. virginiana alba*.

Since the conditions as they appear in the species *R. rugosa* have already been shown, I shall first take up its 3 varieties. *R. rugosa plena* has every appearance of a typical hybrid, as evidenced by a large degree of sterility in its pollen (fig. 14). It seems clear that about 90 per cent of the pollen is abnormal; and the contamination is still more marked when we compare it with *R. rugosa* (fig. 13). *R. rugosa alba* (fig. 15) is not in such bad condition as *R. rugosa plena*, for in this case only about 40 per cent of the grains are

imperfect. *R. rugosa arnoldiana*, a garden variety which is not figured, is in even worse condition than *R. rugosa plena*, having 95–100 per cent of its pollen grains shrivelled and empty.

*R. kamchatica* (fig. 16) shows 50–60 per cent bad pollen. In fig. 16, with the high magnification, the imperfect grains stand out very clearly in contrast to the perfect grains. *R. kamchatica* is native to northeastern Asia, while *R. cordifolia* has its habitat in western Asia and Europe. The latter has very imperfectly developed pollen. *R. oxyodon*, a native of southwestern Asia, also has a quantity of bad pollen (fig. 7). About 75 per cent of that in the loculus is made up of shrivelled, useless grains; and this is typical of the whole species.

*R. rubiginosa* is perhaps the best example found of the phenomena of undeveloped pollen (fig. 6). In this case it is diffiult to find the scattered perfect grains among the host of abnormalities present. The condition is particularly striking when compared with that found in *R. rugosa* (cf. fig. 6 with fig. 5). GRAY (M.) remarks in reference to this species that it is inconstant and suggests relationship to *R. canina*.

ENGLER and PRANTL (Nat. Pflanzenfam.) under the group Cynorrhodeae name several species which have been examined and put in the third group.

> Die Rosen dieser Gruppe sind durch Europa und das Westliche Asien in äusserst zahlreichen Formen verbreitet, welche die Artumgrenzung in vielen Fällen ungemein schwierig machen. *Vielfache Kreuzungen der Arten unter einander, sowie R. gallica* L., *R. alpina* L., *u. s. w. haben zur Mannigfaltigkeit der Formen wesentlich beigetragen.*[5] Als die Hauptarten, um welche sich die verwandten Species gruppieren lassen, können *R. canina* L., *R. rubiginosa* L., *R. mollis* Sm., *R. tomentosa* Sm., und *R. elymaitica* Boiss. betrachtet werden.

I have not figured *R. setipoda* and other species recorded later, but I have examined the pollen of all. *R. setipoda* is a native of Western China, and it is difficult to find a perfect pollen grain in any of its anthers (cf. *R. Moyesii*). *R. mollis* has only about 60 per cent of its pollen grains bad. *R. macrophylla*, a rose from the Himalayas, is in quite as bad a condition as *R. setipoda*. *R. canina biserrata*, a native of Europe found here in both wild and culti-

[5] The italics are the writer's.

vated forms, shows but 10 per cent of the microspores fully formed. *R. arvensis* has only 25 per cent of its pollen grains normally developed. It is often cultivated, and is mentioned by GRAY (F.F.G.) in connection with *R. sempervirens*. The latter is "an Ayrshire rose, evidently an offshoot of *R. arvensis*, a closely related species." In ENGLER and PRANTL (p. 49), under the division with "Kriechende und kletternde Arten," note the following:

*R. repens* Scop. (*R. arvensis* Huds.) wächst auch im westlichen Mittel-Europa wild, während die immergrüne *R. sempervirens* L., den Mittelmeerländern angehört. Von diesen beiden weiss blühenden Arten stammen die kletternden Ayrshire-Rosen welche von den Gärtnern auch mit Theerosen (*R. indica* var.) und anderen Arten gekreuzt worden sind.

*R. gallica*, the cabbage rose, is another interesting species, showing about the same proportion of bad pollen as *R. arvensis*. *R. alba* shows a very large percentage of abnormal grains, and is designated as a "*natural hybrid*" of Europe. *R. damascena* has about 60 per cent of pollen imperfection and is, according to GRAY (F.F.G.), "closely allied to *R. centifolia*." In connection with this species also, GRAY (F.F.G.) says "hybrid perpetual roses are largely derived from this through hybridization with forms of *R. indica* and others."

In reference to the last 3 species described, ENGLER amd PRANTL (Nat. Pflanzenfam., p. 47) furnish some interesting information.

*R. gallica* L., an welche sich *R. damascena* Mill., *R. alba* L., und andere vermeintliche Arten anschliessen, die noch nirgends wirklich wildwachsend nachgewiesen sind und warscheinlich nur als Kulturpfl. existiren. *R. damascena* zeigt eine Annäherung an *R. moschata* Mill., während *R. alba* den Mischlingen aus *R. gallica* und *R. canina* sehr ähnlich ist. . . . . In diesen Formenkreis, dessen Mittelpunkt *R. gallica* ist, gehören alle die edlen, meistens gefüllten Gartenrosen orientalsich-europäischen Ursprungs.

Ganz unabhängig davon ist in Ostasien ein zweiter Formenkreis von gefüllten Gartenrosen gezüchtet worden, welche man auf eine einzige Stammart, *R. indica* L. zurückführt. Neuerdings sind europäische und ostasiatische Kulturrosen vielfach gekreuzt worden. . . . . In den neueren Gartenrosen sind alle diese Arten und Varietäten mit einander verschmolzen worden. Die natürliche lange Blütezeit der *R. indica* hat sich auf manche ihrer Kreuzungsformen vererbt und hat den Anstoss zur Entstehung der lange blühenden und zweimal blühenden Gartenrosen gegeben.

Three species of this last group remain to be mentioned. *R. setigera* shows a large percentage of microsporic degeneracy. *R. virginiana plena* with about 90 per cent of its pollen bad, and *R. virginiana alba* with but 25 per cent of its pollen imperfect, are varieties of the *R. virginiana* Mill. of GRAY'S *Manual*. The latter, known sometimes as *R. lucida* Ehrh., is a dwarf wild rose found on the margins of swamps and rocky shores from Newfoundland and eastern Quebec to New York and eastern Pennsylvania.

The preceding statistics show clearly that the species of *Rosa* are in a very marked degree characterized by abnormal pollen. It is true likewise that abnormal pollen is largely sterile. Pollen sterility for nearly a hundred years has been recognized by plant breeders as a prominent characteristic of hybrids; and another well known characteristic of hybrids is their extreme variability. Since both extreme pollen sterility and variability are prominent features of hybrids, the conclusion seems inevitable that most of the so-called species of *Rosa* are in reality hybrids.

This conclusion is most interesting when viewed from an evolutionary standpoint. Are new species the result of gradual changes or sudden leaps? The answer to this depends largely upon the definition of the term species. In the lower vascular plants the conditions of spore abortion and hybridization appear to be very rare. The term species in these cases, therefore, is used to distinguish groups of plants wholly distinct from one another and probably genetically pure. JEFFREY[6] has shown by microscopical investigation that morphologically sterile pollen does not occur in plants that are monotypic, isolated geographically or through the time of flower maturity. He has likewise made a comparison of the "conditions of sporogeny found in the lower plants, the Bryophyta, Pteridophyta, and gymnosperms, which are not characterized by enormous multiplication of species, with the sporogenic features of the angiosperms in which multiplication of species has run riot." In this comparison he found that in the lower forms of Embryophyta, from the Bryophyta to the gymnosperms, "infertile spores and hybridism were conspicuous by their

[6] JEFFREY, E. C., Some fundamental morphological objections to the mutation theory of DEVRIES. Amer. Nat. **49**:5–21. *figs.* 7. 1915.

absence." Among the gymnosperms he examined Cycadales, Ginkgoales, Coniferales, and Gnetales, and found "a single species of *Abies* with evidence of abortive pollen grains of hybrid origin."

The photomicrographs of *Lycopodium complanatum* and *Pinus divaricata* (figs. 1, 2) show clearly the morphological condition typical in both genera, fertile spores uncontaminated by any abnormal, sterile grains. JEFFREY states that "the genus *Pinus* is very old and its species accordingly very distinct"; and he has not yet found "the slightest evidence of hybridization here or in other numerous and widely distributed species of conifers, other than the *Abies* mentioned above."

In the angiosperms, on the contrary, hybridism as a condition widespread in nature is commonly recognized. For example, in this country and in Europe systematic botanists agree that hybridism is extremely common as a natural condition in certain genera of the Rosaceae. BRAINERD has shown that a great many "natural hybrids" of *Rosa* and *Rubus*, occur; and JEFFREY[7] in a recent article says as follows:

> Not only are certain of the Rosaceae recognizable as hybrids on account of their transitional external features of organization, Mendelian phenomena, etc., but certain others which have not revealed themselves as hybrids in these ways are clearly such as a result of a study of their spores. . . . . Taking morphological features into account, as well as the data of the systematic botanists, there are three kinds of individuals; pure species, recognized species with pollen showing they are concealed hybrids or crypthybrids, and recognized hybrids or phenhybrids.

These 3 classes, typical of many angiospermous genera, make it difficult to determine what individuals shall form a species. In the higher vascular plants, therefore, the term species is obviously used in a very different sense from that in which it is applied to the lower vascular plants. Clearly crypthybrids should not be species in the same sense in which the name is used of *Pinus* and other morphologically normal genera. But they are generally admitted by the systematist as good species because of their relative constancy and the absence of observed intergrading types, though the morphological conditions are undoubtedly those of hybrids.

[7] JEFFREY, E. C., Spore conditions in hybrids and the mutation hypothesis of DEVRIES. BOT. GAZ. **58**:322–336. *pls. 22–25.* 1914.

Now if crypthybrids could *justly* be called true species, it might possibly be admitted that they to some extent support the mutation theory of DEVRIES. But unfortunately they are frequently, although not universally, very variable, and this variability would appear on morphological grounds to be the result of hybridization.

On the other hand, the natural hybrid or phenhybrid found in the angiosperms and resulting from a cross between distinct species, with no segregation as in Mendelian crosses, but a blending of the parent characters, may breed true to these respective characters, in which case a new and distinctive form is perpetuated, and to this the systematist may justly give a specific rank. Such forms, however, are usually characterized by a large amount of sterile pollen, unlike the true species in which the pollen is morphologically perfect. Hence the term species is used here in a sense somewhat different from that ordinarily implied.

In proportion to the extension of the term species, the number of species has grown astonishingly. This multiplication of species is probably largely due to hybridization, judging from the morphological data afforded by the Rosaceae; and generally the new "species" are crypthybrids. HOAR[8] of this laboratory has been investigating *Rubus* and has reached results corresponding to those recorded here with regard to *Rosa*. Hybridism appears to be even more rife in *Crataegus*, and the multiplication of species is likewise greater, as is shown by the result of work carried on by Miss LORA STANDISH.[9]

It is interesting to note how many of the species of the genus *Rosa* in cultivation at the Arnold Arboretum are really crypthybrids, and how many are true species and phenhybrids. Take the 3 groups as presented according to their pollen sterility. To the first group only can the term species be accurately applied, that is, in the strict sense of the word as used of species of *Pinus* and *Lycopodium;* for only in this group is the percentage of sterile pollen so negligible that the members may be considered, with some degree of probability, genetically pure.

[8] HOAR, C. S., Sterility as the result of hybridization and the condition of the pollen in *Rubus*. BOT. GAZ. **62**: 370–388. 1916.

[9] STANDISH, LORA, What is happening to the hawthorns? Jour. Heredity **7**: 266–279. 1916.

In the second group there are 3 phenhybrids and 3 garden varieties probably of hybrid origin though not so designated. The remaining 14 are crypthybrids, several of which are treated as species in standard systematic works; as for example, *R. blanda* with 20 per cent of its pollen grains abortive, and *R. rubiginosa* with pollen almost completely undeveloped.

In the third and last group I find 3 phenhybrids; one natural hybrid of known parentage, *R. alba;* two recognized hybrids, *R. rubiginosa* regarded as derived from *R. canina*, and *R. damascena* which is allied to *R. centifolia* and parent with *R. indica* of "hybrid perpetual roses"; and two garden varieties of *R. rugosa* which are also of recognized hybrid origin. The remaining 12 of this group are crypthybrids.

These crypthybrids of *Rosa* are particularly interesting in connection with the several theories of the origin of species. We know that they are common not only in the Rosaceae, but, as has been shown to be probable, also in the Onagraceae and other families of the angiosperms. Such forms, though recognized as species, obviously cannot rank with pure species in the sense in which that term is applied to gymnosperms, etc., in evolutionary discussions; for, as JEFFREY has recently stated (see footnote 6), "The conduct of such forms is conditioned more or less by their mixed blood."

In this connection it is interesting to note the conditions presented by *Oenothera Lamarckiana* and other species of the genus as described by DEVRIES and other authors. Here we have, as is the case in *Rosa*, a considerable degree of variability accompanied by a large amount of pollen sterility. Upon *Oenothera* and forms manifesting similar peculiarities DEVRIES has mainly based his mutation hypothesis.

To go back to the original question, are new species the result of gradual changes or sudden leaps? The Darwinian hypothesis, as has been pointed out, is in large measure supported by the species of *Pinus*. But, as I have shown, the term species when used of *Pinus* has an altogether different significance from that which it has when used of *Rosa;* and consequently, the problem of evolution as presented by the species of *Rosa* must be an entirely

different one. There must be careful distinctions made between the 3 classes of individuals; and the search for the true solution of the problem of the origin of species becomes thereby a matter of great complexity. As for the mutation hypothesis of DEVRIES, the morphological and systematic evidence set forth with regard to the conditions in *Rosa*, and the similar conditions brought out with regard to *Rubus*, *Crataegus*, and the Rosaceae as a whole, seem to lend it little support, since the mutability here is obviously the result of hybridization in nature.

## Conclusions

1. The species of *Rosa* are characterized by a large amount of abortive pollen and also by great variability.

2. Both pollen sterility and variability have long been recognized as two main characteristics of hybrids.

3. The species of *Rosa*, therefore, are largely of hybrid origin.

4. On account of the great number of crypthybrids and phenhybrids in angiosperms, the term species has a very different meaning from that which it has when applied to the lower vascular plants and the gymnosperms.

5. The mutability of the species of *Rosa* cannot properly be used in support of the mutation hypothesis, since this phenomenon is obviously the result of hybrid contamination in nature.

In conclusion the writer wishes to express her most sincere thanks to the Director of the Arnold Arboretum for permission to collect material; and to Professor E. C. JEFFREY for advice and assistance.

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## EXPLANATION OF PLATES IV–VI

*PLATE IV*

FIGS. 1–6.—Pollen.

FIG. 1.—*Lycopodium complanatum;* ×125.

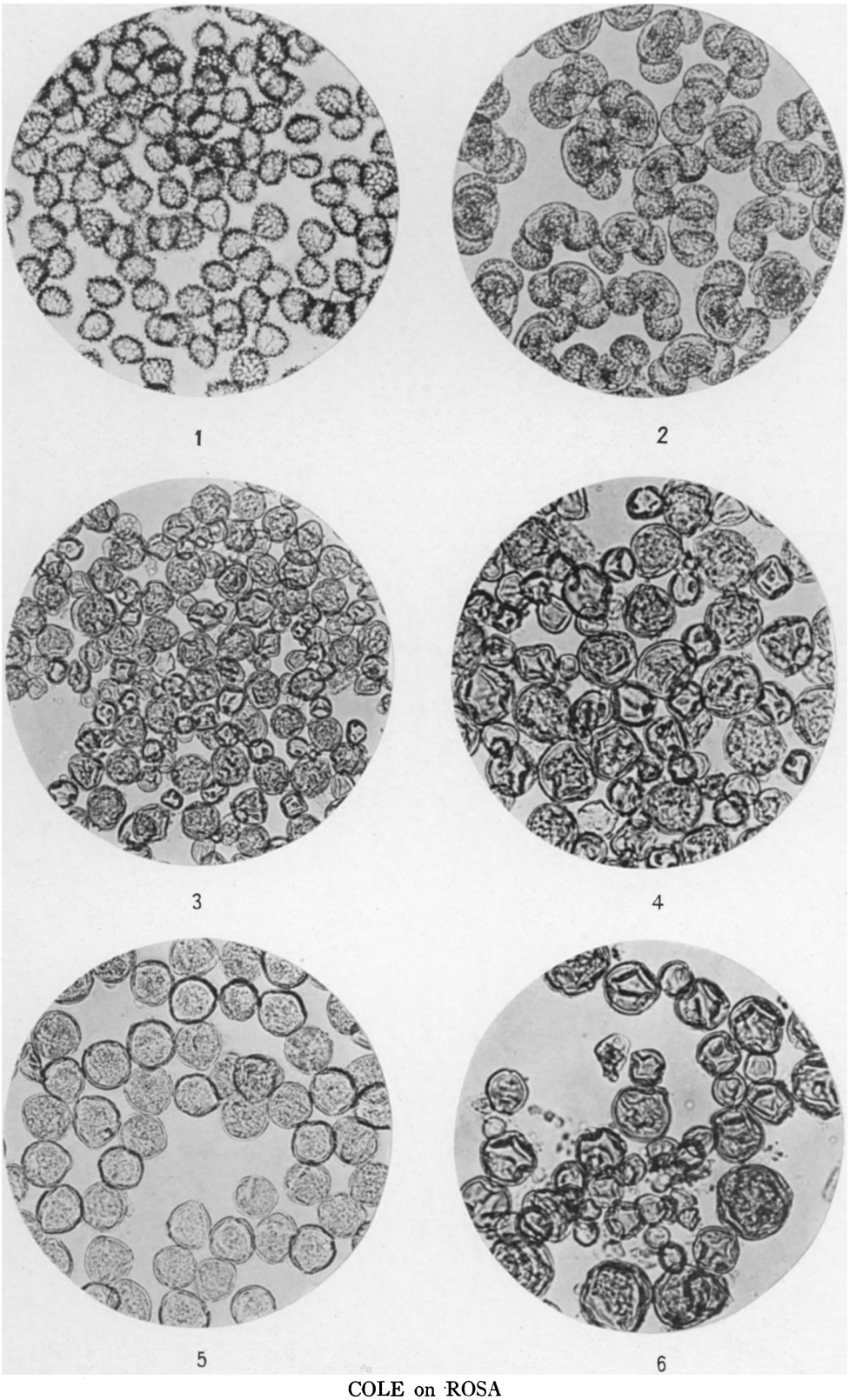
FIG. 2.—*Pinus divaricata;* ×125.

FIG. 3.—*Rosa alba;* ×250.

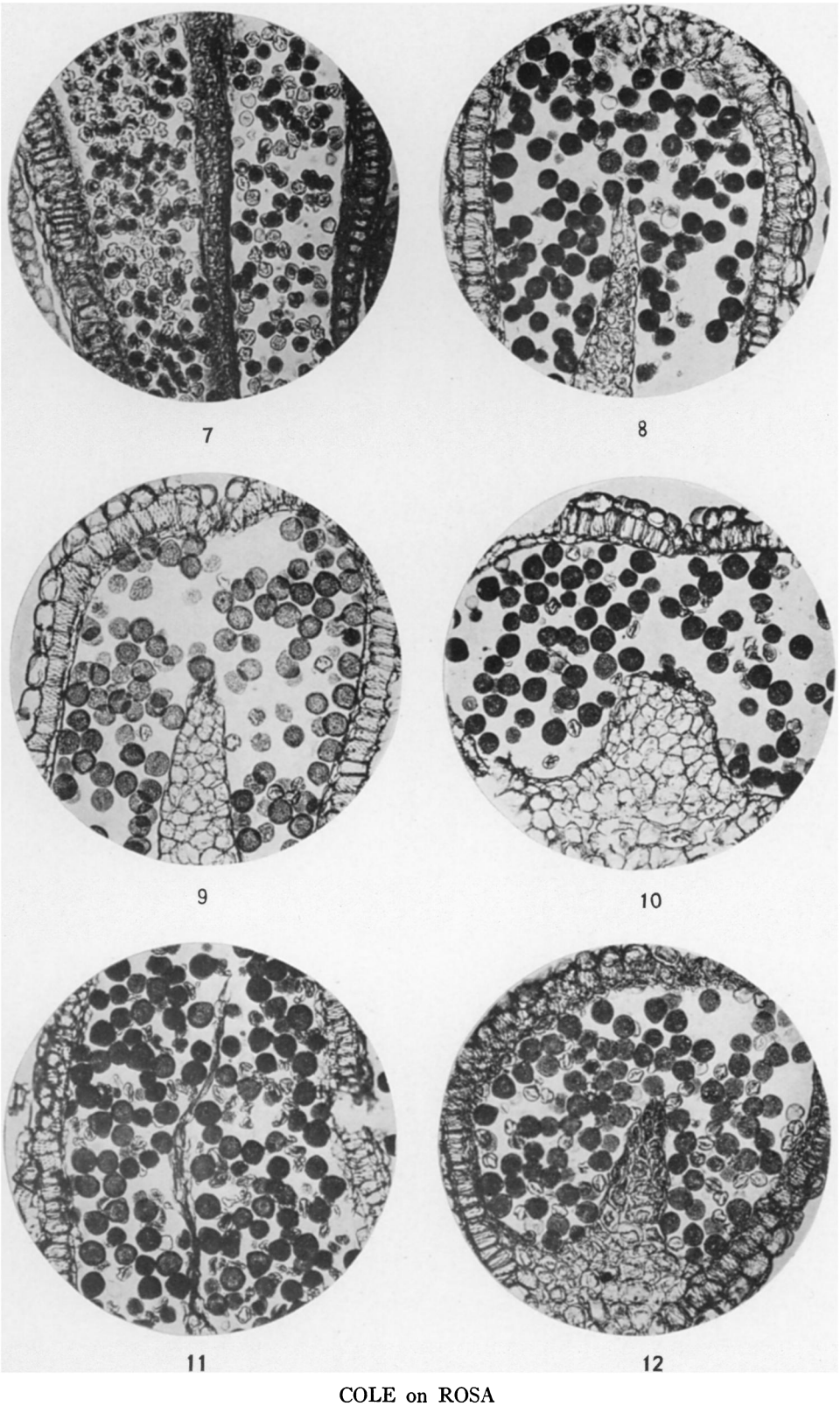
FIG. 4.—*Rosa alba;* ×375.

FIG. 5.—*Rosa rugosa;* ×250.

FIG. 6.—*Rosa rubiginosa;* ×375.




COLE on ROSA

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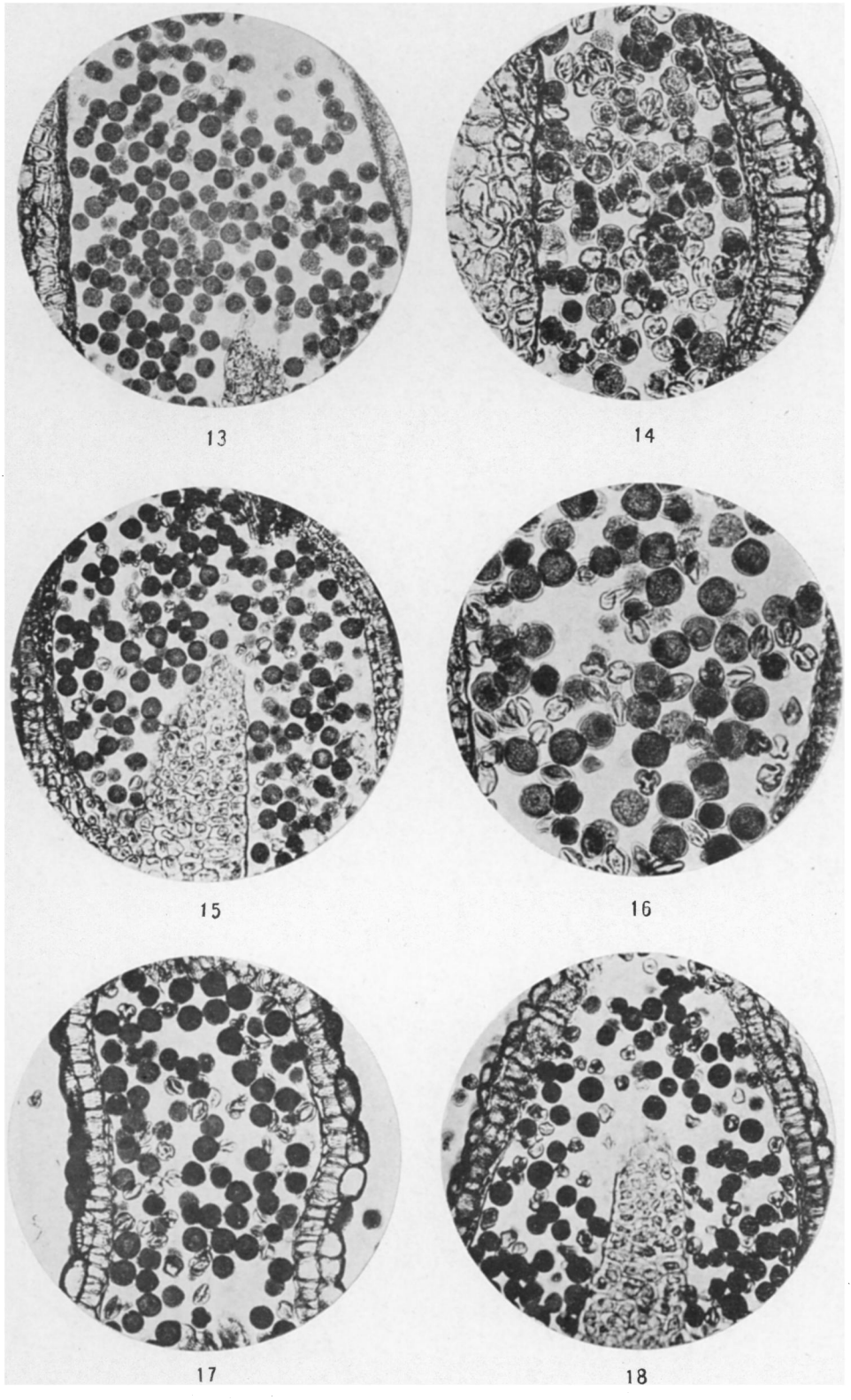


COLE on ROSA

*PLATE V*

FIGS. 7–18.—Transverse sections of anther.
FIG. 7.—*Rosa oxyodon;* ×125.
FIG. 8.—*Rosa spinosissima altaica;* ×125.
FIG. 9.—*Rosa spinosissima hispida;* ×125.
FIG. 10.—*Rosa spinosissima* (gard. var. hyb.); ×125.
FIG. 11.—*Rosa spinosissima fulgens;* ×125.
FIG. 12.—*Rosa spinosissima;* ×125.

*PLATE VI*

FIG. 13.—*Rosa rugosa;* ×125.
FIG. 14.—*Rosa rugosa plena;* ×125.
FIG. 15.—*Rosa rugosa alba;* ×125.
FIG. 16.—*Rosa kamchatica;* ×250.
FIG. 17.—*Rosa Manetti;* ×125.
FIG. 18.—*Rosa Harrisoni;* ×125.